Ecology and cultivation of the herbivorous brackish-water nematode Eudiplogaster pararmatus

Romeyn, K; Bouwman, LA; Admiraal, W

Published in:
Marine Ecology Progress Series

DOI:
10.3354/meps012145

Publication date:
1983

Vol. 12: 145–153, 1983 | MARINE ECOLOGY – PROGRESS SERIES
Mar. Ecol. Prog. Ser. | Published May 30

Ecology and cultivation of the herbivorous brackish-water nematode *Eudiplogaster pararmatus*

K. Romeyn, L. A. Bouwman and W. Admiraal

Biological Research Ems-Dollard Estuary, Department of Systematic Botany, State University of Groningen, P.O.Box 14, 9750 AA Haren, The Netherlands

ABSTRACT: The sediment inhabiting rhabditid nematode *Eudiplogaster pararmatus* (W. Schneider 1938), is a halophilic member of the family Diplogasteridae (non-marine animals, often occurring in saprobic environments). It colonizes successfully the waste-water exposed intertidal mud flats in the southeast of the Ems-Dollard estuary, The Netherlands. Microscopic observations in agar cultures witness that *E. pararmatus* feeds on diatoms. The nematode consumed representatives of 7 different diatom species by puncturing their frustules and swallowing their contents. Adults consumed about 7 cells h^{-1} of *Navicula salinarum* (Grunow). Comparable consumption rates were calculated from experiments by other researchers, with ^{14}C labelled diatoms. The reproduction and population growth of *E. pararmatus* were studied in cultures with various salinities and diatom densities at a temperature of 17 °C. Reproduction occurred under almost all conditions but the number of nematodes increased importantly only in cultures with low salinities (0.5 to 2.5 ‰ S) and food densities of over 2×10^6 cells cm^{-3}. Growth of individual nematodes was studied at 2 different temperatures in agar cultures with low salinities and adequate food. Temperature appeared to govern the moment of sexual differentiation: at 12 °C, this differentiation occurred after approximately 2.5 wk; at 21 °C, after only 1.5 wk. Generation times observed in cultures varied between 45 d (at 12 °C) and 21 d (at 21 °C); this is in the same range as the generation time found for other brackish water and marine nematodes with a similar life style. Tentative calculations of the reproductive rate of exponentially growing populations in the field (in spring, 12° to 18 °C), revealed a generation time of 25 to 33 d; this is slightly shorter than the generation time observed in cultures. Brief exposure to high temperatures during emersion of the flats may be responsible for this difference.

INTRODUCTION

Previous studies on the feeding biology of marine and brackish water nematodes have been concerned with predatory and bacteria-consuming species (Wieser and Kanwisher, 1959, 1961; Hopper and Meyers, 1966b; Tietjen and Lee, 1972; Grootaert and Maertens, 1976; Heip et al., 1978; Lopez et al., 1979). Hardly any comparable studies have been made on herbivorous nematodes, probably because their cultivation is more difficult. Although several authors (Wieser, 1953; von Thun, 1968; Tietjen et al., 1970; Lee et al., 1977) have noted that brackish water nematodes consume diatoms, details of the feeding behaviour and grazing rates (=feeding rates) of these herbivores have been insufficiently explored. Studies on nematodes living on the brackish water mud flats of the Dollard (Fig. 1; Bouwman, 1978, 1981/in press; Romeyn, 1980) indicate that diatoms constitute an important fraction of their diet. This study presents detailed information on the herbivorous nematode *Eudiplogaster pararmatus* (W. Schneider, 1938), a halophilic member of the family of the Diplogasteridae (mostly nonmarine terrigenous animals often occurring in saprobic environments (Schneider, 1939; Schiemer, 1975). *Eudiplogaster* (Fig. 2) is a dominant species that occurs in large numbers (up to 1400 individuals cm^{-2}) on the organically polluted mud flats in the south-east of the Dollard (The Netherlands) where several diatom species are also found in large numbers.

Publication No. 58 of the project Biological Research Ems-Dollard Estuary, 1983

0171-8630/83/0012/0145/$ 02.00

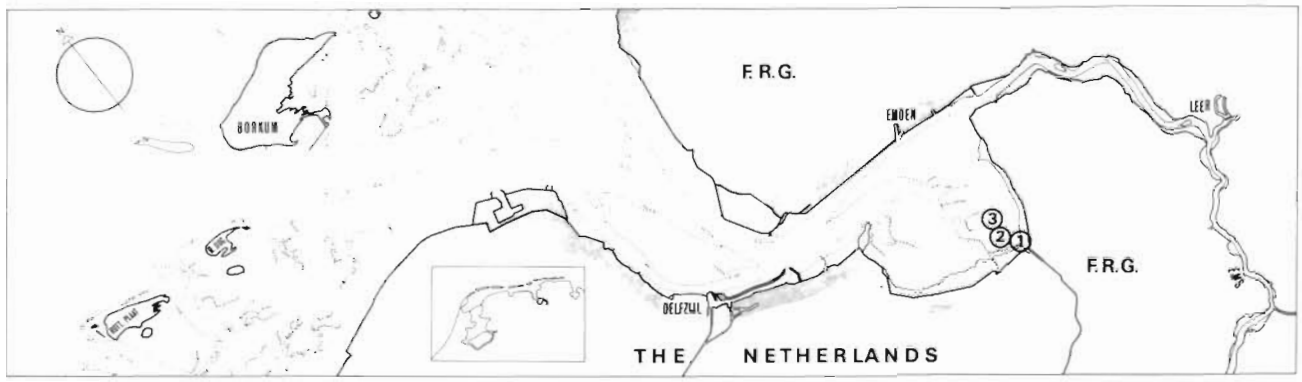

Fig. 1. Location of 3 sampling Stations on the 'Oostfriesche Plaat' intertidal flat in the Ems-Dollard estuary, The Netherlands

MATERIAL AND METHODS

Natural habitat of *Eudiplogaster pararmatus*

The tidal flats in the south-eastern part of the Dollard (Fig. 1) are situated high in the tidal zone and emerge for the greater part of a tide, particularly during strong eastern winds. Desiccation of the sediment and large fluctuations in temperature and salinity occur. A large amount of organically polluted water is discharged into this part of the estuary by the river Westerwoldse Aa (van Es et al., 1980). The sediment of the flats contains a high proportion of detritus and clay (Schröder and van Es, 1980). Anaerobic conditions prevail in the sediment caused by rapid mineralization of organic material present in the overlying water.

Together, these factors are responsible for extreme habitat conditions, with macrofauna elements almost entirely absent (van Arkel and Mulder, unpubl; Essink and Kleef, unpubl; van Es et al., 1980); only a few meiofauna species are able to survive (van Es et al., 1980; Bouwman, 1981/in press).

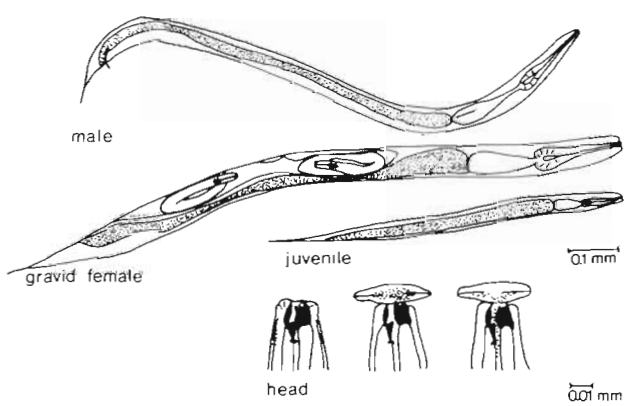

Fig. 2. *Eudiplogaster pararmatus*. Habitus and punctation of a diatom and removal of its contents

Sampling

In 1980, samples were collected monthly from 3 sampling stations: 2 stations (1 and 2; Fig. 1) were close to the freshwater discharge point and characterized by large densities of nematodes and a low number of species; the other station (3), was situated 3 km from the discharge point, where the nematode population was more diverse and lower densities of nematodes were found. Four replicate sediment cores ($\varnothing$ 4.52 cm^2) were taken to determine the amount of nematodes in the top-layer (0 to 1 cm) of the sediment (c.f. Bouwman, 1981/in press). For the present study, the total number of all nematodes as well as the number of *Eudiplogaster pararmatus* were determined. The nematodes were separated from the sediment using the Ludox T. M. flotation method (de Jonge and Bouwman, 1977). Sieves with a mesh size of 30 µm were used.

Cultivation

Large numbers of *Eudiplogaster pararmatus* were collected and kept in the dark at a low temperature (4 °C) in artificial seawater (Admiraal, 1977) with a salinity of 5 ‰ S. The seawater was changed every 4 to 5 d. Food (e.g. diatoms) was not added; it was possible to keep *E. pararmatus* alive in these non-sterile stock cultures for more than 1 yr.

Attempts to rear *Eudiplogaster pararmatus* in a liquid culture containing coarse-grained sand and diatoms failed. Incubation of *E. pararmatus* in agar cultures containing diatoms facilitated reproduction. The following procedure was used: agar cultures (Difco bacto agar, Detroit, USA) with a salinity of 5 ‰ S were prepared. Molten agar (5 g l^{-1} water) was mixed with a diatom suspension, on a vortex mixer at a temperature of 35 °C. Droplets (0.5 cm^3) of the molten

agar were pipetted into Petri dishes (Ø 35 mm). All diatom species used survived this treatment. The nematodes were inoculated into the solidified agar with a bamboo needle. The Petri dishes were sealed with parafilm and placed on a tray in a perspex box, partly filled with water to prevent desiccation of the cultures. The cultures were incubated at 17 °C, with 16 h light d^{-1}.

Microscopic observations and growth parameters

The feeding behaviour of *Eudiplogaster pararmatus* was studied with an inverted microscope, using small observation chambers (Type B; Maertens, 1975) filled with a thin layer of agar that contained several different species of diatoms. Magnifications up to 400 times (40 × 10) were used. The feeding behaviour of *E. pararmatus* on the diatom *Gyrosigma spenceri* was recorded on 16 mm film which is available on request ('Grazing of nematodes in intertidal flats'. Romeyn, K. and L. A. Bouwman, in press, Dienst Beeld en Geluid. State University of Groningen, The Netherlands). Several species of diatoms, all occurring attached to the sediment at the sampling sites, were cultured (c. f. Admiraal, 1977): *Navicula salinarum* (Grunow), *N. pygmaea* (Kützing), *N. cf. cryptocephala* (Kützing), *N. phyllepta* (Kützing), *Nitzschia sigma* (Kützing) W. Smith, *N. cf. thermalis* (Ehrenberg) Grunow, *Gyrosigma spenceri* (W. Smith) Cleve, and *Surirella ovata* (Kützing).

Ciliates, small flagellates and amoebae (occurring in old agar cultures and in old diatom cultures and easily raised in agar mixed with diatoms) were also given to *Eudiplogaster pararmatus* in observation chambers. The size of *E. pararmatus* populations in cultures was determined by counting the nematodes under a stereo microscope. Growth experiments with different food densities, different salinities and different temperatures were carried out with 3-wk old nematodes.

To ascertain the growth of individual nematodes, their body-volume was calculated from length and width measurements, using the formula:

$$V = \frac{1}{3} \cdot \pi \cdot R^2 \cdot h_1 + \pi \cdot R^2 \cdot h_2 + \frac{1}{3} \cdot \pi \cdot R^2 \cdot h_3$$

The nematode is considered to be a cylinder with a radius R and a length h_2, with two conical ends with the same basal radius R and a length of h_1 and h_3 respectively.

Generation time in culture was determined by cultivating juveniles of known age until a new generation was born (*Eudiplogaster pararmatus* is viviparous; Fig. 2). The generation time in field populations was calculated using the following equation (Heip et al., 1978):

$$G = \frac{1}{r} \cdot \ln (p \cdot Ne)$$

where G = generation time in d; p = fraction of females in the population; Ne = number of juveniles ('born') per female; r = intrinsic rate of natural increase. r was calculated by the equation (Fenchel, 1974; Tietjen and Lee, 1977):

$$N_t = N_o \cdot e^{r \cdot t}$$

where N_o = population size at time o; N_t = population size at time t.

RESULTS

Observations on the feeding behaviour of *Eudiplogaster pararmatus*

In liquid medium, *Eudiplogaster pararmatus* wriggled continuously, without displacing itself very much. Under these conditions a nematode is not able to 'catch' diatoms. It pushed the diatom cells away and did not succeed in puncturing them. In contrast, *E. pararmatus* moved rather sluggishly in agar, even in watery agar, continuously making small movements with its head, until it collided with a particle. If this particle was a sand grain or a diatom cell, the oesophageal pump of the nematode started working. The pumping movements probably play a role in the puncturing of diatom cells (see 'Discussion'). If the particle was a sand grain, the pumping stopped after several attempts. If the particle was a diatom cell the nematode apparently punctured the cell (the actual pumping could not be observed) and kept pumping until the contents of the diatom were swallowed. Contents of all diatom species tested (except *Navicula pygmaea*) were swallowed easily. It appeared to be difficult for *Eudiplogaster pararmatus* to puncture the frustules of *N. pygmaea* and to swallow its contents. Sometimes the nematode succeeded in puncturing a cell but managed to suck out only a small part of the contents after approximately 30 pumping movements of the oesophagus, while only 3 to 5 pumping movements were observed during the consumption of the other diatoms offered.

Length and size of the diatom cells did not seem to be very important. Small diatoms, such as *Navicula cf. cryptocephala* and *Surirella ovata* were punctured as easily as the large cells of *Gyrosigma spenceri*. The nematode punctured the diatom at the top or in the middle of the frustule, probably just in the raphe.

During 5-h periods of microscopic observations, adult nematodes consumed 30 to 35 cells of the diatom *Navicula salinarum* in agar cultures containing approximately 2×10^6 diatom cells cm^{-3}. Ciliates,

flagellates and amoebae were not eaten. Even in viscous agar, in which the ciliates and flagellates could not move very fast and *Eudiplogaster pararmatus* frequently collided with them, no pumping activity was observed. Possibly, these soft organisms did not offer enough resistance to induce pumping. The mucus layer that envelopes the amoebae may prevent the nematode from gripping it.

Effects of diatom density, salinity and temperature on growth of *Eudiplogaster pararmatus* in agar cultures

To study the effect of food density on a nematode population, several population densities of *Navicula salinarum* were offered to initial populations of 25 3-wk old nematodes (Fig. 3). For sustaining a popula-

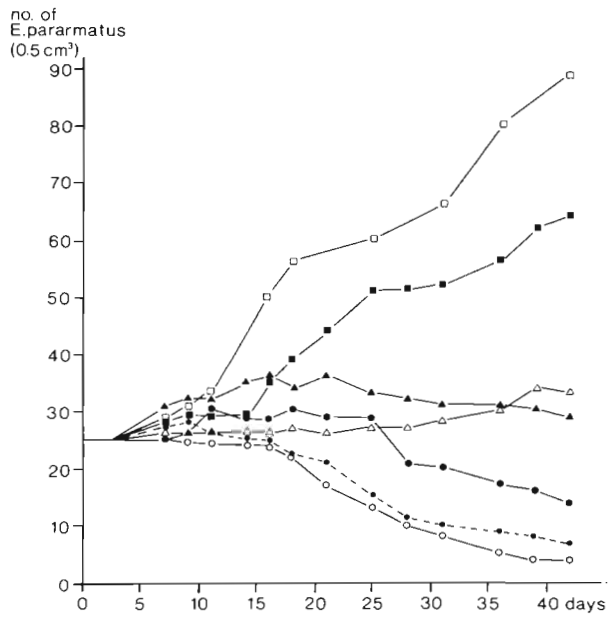

Fig. 3. *Eudiplogaster pararmatus*. Population growth in agar cultures supplied with bacteria (●—●) and different densities of the diatom *Navicula salinarum*: 6×10^6 cells cm^{-3} □, $4 - 10^6$ cells ■, 2×10^6 cells △, 1×10^6 cells ▲, 0.1×10^6 cells ●--● and 0 cells cm^{-3} ○

tion of *Eudiplogaster pararmatus*, a minimum density of 2×10^6 diatom cells cm^{-3} appeared to be necessary. To obtain an obviously growing population, the density of diatom cells should exceed 2×10^6 cells cm^{-3}. In cultures containing a few (0.1×10^6 cells cm^{-3}) or no diatoms, the nematode population decreased rapidly. In agar cultures enriched with glycine (0.25 %), which stimulated bacterial growth, and in cultures with a small amount (1×10^6 cells cm^{-3}) of diatoms added, the number of nematodes remained unchanged for about 3 wk but then decreased.

To study the effect of salinity on the growth of *Eudiplogaster pararmatus* populations, the nematode was cultured in agar of different salinities and a sufficient amount of *Navicula salinarum* as food (Fig. 4). Salinities of 0.5 to 20 ‰ S permitted growth of the nematode populations. However, close to optimal growth is restricted to 0.5 to 2.5 ‰ S, the salinity at which *E. pararmatus* is most frequently found in the field.

To study the effect of temperature on the growth of individual nematodes, observations were made on young nematodes, kept at 2 different temperatures (Fig. 5). In the first week after hatching, growth of juveniles at 21 °C was less than that at 12 °C. At 21 °C, rapid growth occurred from the 10th day onwards, eventually leading to larger worms (larger calculated volumes) than at 12 °C. At both temperatures the volume of individual females was higher than that of

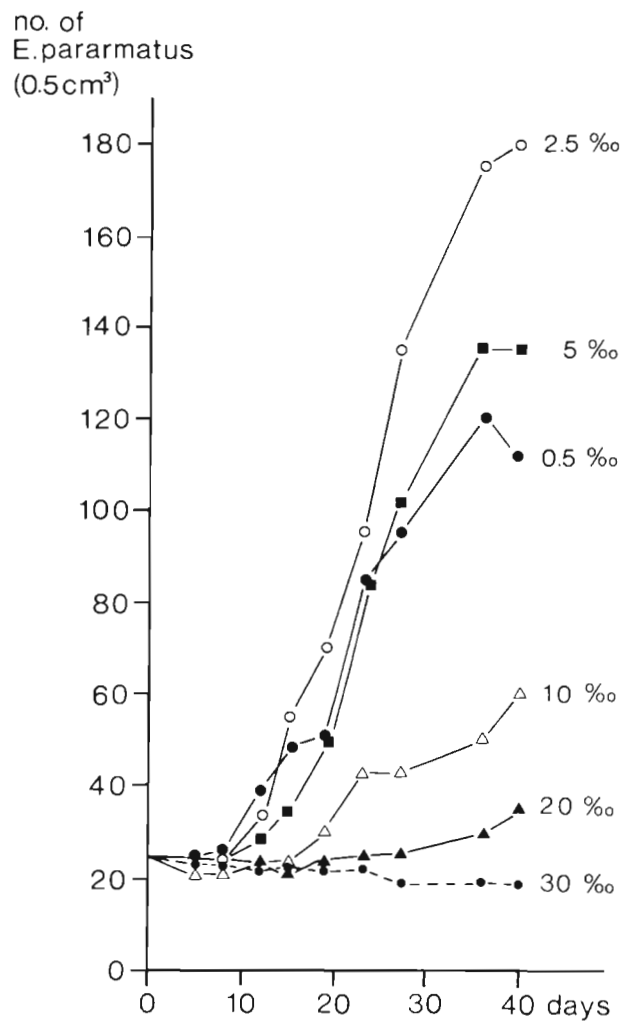

Fig. 4. *Eudiplogaster pararmatus*. Population growth in agar cultures of different salinities (0.5 to 30 ‰) containing diatoms (*Navicula salinarum*, ca. 4×10^6 cells cm^{-3})

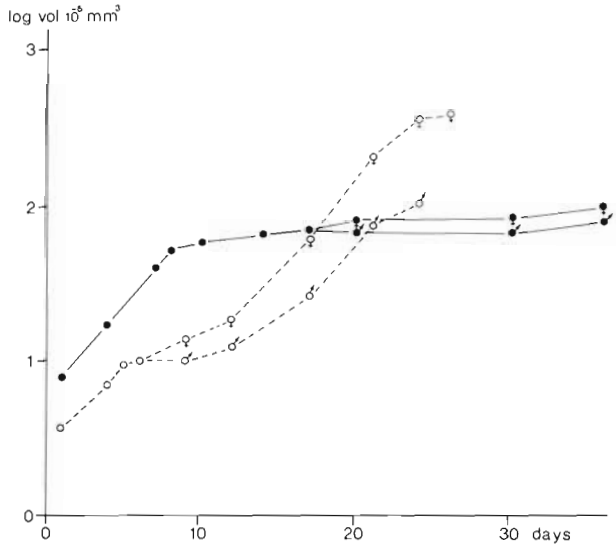

Fig. 5. *Eudiplogaster pararmatus*. Mean increase in volume of individuals at 2 different temperatures (12 °C, ○ and 21 °C, ●)

males. At 21 °C, reproductive organs appeared already after ca. 1.5 wk, while at 12 °C reproductive organs could be distinguished after ca. 2.5 wk. Generation times (1-d old juveniles were cultivated until new offspring was born) observed in agar cultures with low salinities and adequate food varied between 45 d at 12 °C and 21 d at 21 °C.

Population size and structure of field populations

The total number of *Eudiplogaster pararmatus* in the observation area varied: at Stations 1 and 2 high numbers were found (especially in spring and summer; Fig. 6), while at Station 3 hardly any *E. pararmatus* occurred (Fig. 6). At Stations 1 and 2 the population grew rapidly from 100 to 1000 individuals cm^{-2} in late spring. During summer, numbers were high. In autumn, population size decreased and stabilized at low numbers (30 to 50 ind. cm^{-2}) which persisted during winter.

For almost the whole year, females outnumbered males at Stations 1 and 2 (Fig. 7). From February to May, the ratio of males to females was strongly in favour of the females, while in June and July the difference between the number of males and females was less obvious. The mean ratio of males to females was 1:2. The ratio of gravid females to non-gravid females was >1 during most of the year.

Juveniles were present throughout the year, suggesting continuous reproduction. Gravid females contained 10 to 12 juveniles from May to June (as observed in previous years; Romeyn, 1980). The total

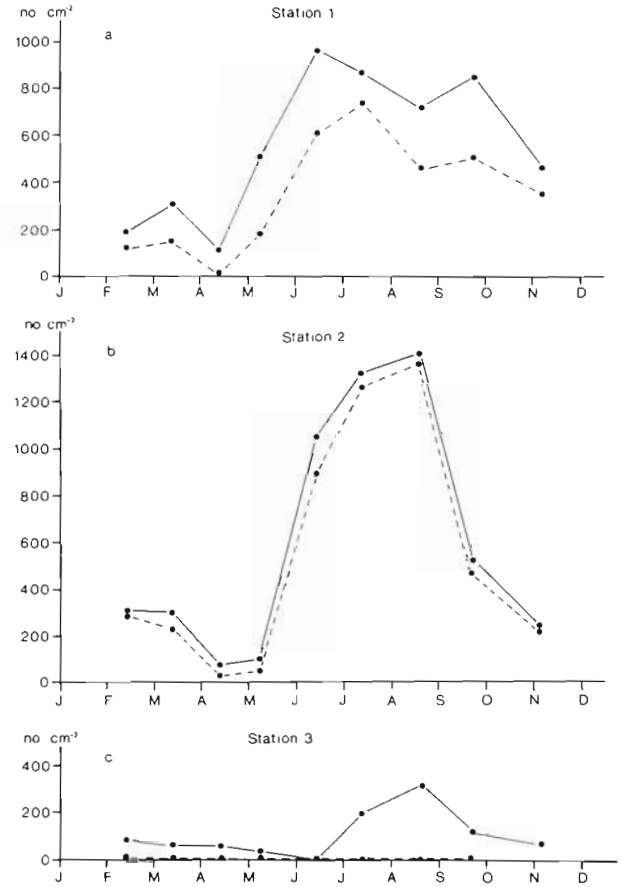

Fig. 6a, b, c. Total number of nematodes (●—●) and number of *E. pararmatus* (●--●) at the sampling Stations in 1980

number of juveniles in the population was underestimated because juveniles inside the gravid females were not taken into account.

Tentative calculations of reproductive rate of field populations

The population of *Eudiplogaster pararmatus* increased rapidly during spring (Fig. 6). Assuming that during this relatively short period population growth is not greatly affected by predation, mortality or food limitation, reproductive rate in natural populations can be tentatively calculated using the equation by Fenchel (1974) and Tietjen and Lee (1977).

The highest reproduction rate in the population at Station 2, occurred from May to June: a population of 50 nematodes cm^{-2} increased within 36 d to a population of 900 nematodes cm^{-2}. For this period the intrinsic rate of increase (r) was calculated to be 0.08. The population at Station 1 reproduced rapidly from April to May, the r value being ca. 0.06. There were fewer *E. pararmatus* at Station 1 than at Station 2.

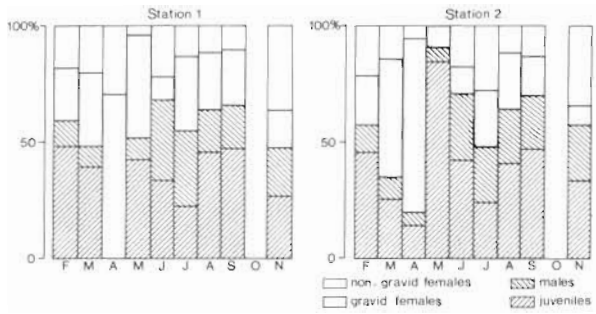

Fig. 7. *Eudiplogaster pararmatus*. Proportion of males, females and juveniles at Stations 1 and 2 in 1980

Generation time can be calculated using the equation by Heip et al. (1978). The average number of juveniles per female (N_e) was 11, the mean proportion of females in the population (juveniles excluded) was ca. 69 % (Fig. 6; 68.1 % at Station 1; 69.6 % at Station 2); this means that $p = 0.69$. Generation time for periods of maximum population growth were at Station 1, G = 33.8 d and at Station 2, G = 25.3 d.

DISCUSSION

Feeding behaviour

According to Wieser's (1953) tentative classification of nematodes on the basis of the form and armature of the buccal cavity, *Eudiplogaster pararmatus* is an epigrowth feeder. Our microscopical observations confirm this.

In searching for its food, *Eudiplogaster pararmatus* does not seem to be attracted by specific traces of food, e.g. excretion products of algae and bacteria, as mentioned by Dusenberry (1974) and Hellebust (1974). Searching for food seems to be a 'trial and error' process (Hopper and Meyers, 1966a). *E. pararmatus* makes small movements with its head until it collides with a particle. Obviously, the nematode can distinguish between rigid and soft particles: a collision with a rigid particle (e.g. a diatom) triggers the pumping mechanism whereas a soft particle (e.g. an amoeba) does not. Probably the rigidity of the latter is insufficient for activating the pumping mechanism of the nematode. Rigid particles such as sand grains induce pumping; at the same time the nematode attempts to puncture the particle and to remove its contents. Since *E. pararmatus* is not able to puncture a sand grain, pumping ceases after several attempts. The only remaining 'suitable' food consists of diatoms; these the nematode punctures before swallowing their contents.

Not all diatoms appeared to be suitable as food for *Eudiplogaster pararmatus*: the diatom *Navicula pygmaea* was not consumed easily. Structure and rigidity of a particle seem to be important factors for *E. pararmatus* to discriminate among different food particles (after colliding with them). The size of the particles seems to be unimportant (in contrast to the suggestion of Tietjen and Lee, (1973)).

The 'trial and error' searching method is efficient only when the density of suitable diatoms is high. Where diatom densities are low or the diatoms present less edible, more energy has to be invested in feeding and less energy will be available for growth and reproduction. This conclusion is confirmed by experiments with different densities of suitable food (*Navicula salinarum*). Comparable experiments with the less edible species *N. pygmaea*, resulted in fewer juveniles, slower growth of juveniles and a longer generation time (Hoekstra, unpubl.). Adult *E. pararmatus* consumed about 7 diatoms h^{-1}. Other feeding experiments, using ^{14}C labelled diatoms (*N. salinarum*) for 1 to 4 h, yielded a similar value (Admiraal et al., 1983). However calculations of total consumption of field populations of *E. pararmatus*, based on consumption rates in agar cultures, should be interpreted with care because feeding rates and feeding behaviour under field conditions may differ from those recorded under laboratory conditions.

It is possible that under particular circumstances *Eudiplogaster pararmatus* is able to use also food sources other than diatoms. Schiemer (1975) mentioned bacteria consumption and intake of dissolved organic material by several species of the family Diplogasteridae, occurring in used-water treatment plants. Preliminary results from experiments with labelled bacteria and with labelled organic molecules (amino acids; Kremer et al., unpubl.) suggest that it is unlikely that *E. pararmatus* consumes bacteria but it seems possible that it takes up organic molecules (compare Chia and Warwick, 1969; Riemann and Schrage, 1978). The latter may be responsible for the long survival of *E. pararmatus* in non-sterile liquid cultures without diatoms at low temperatures (4 °C); the excretion products of bacteria and even of the nematodes themselves (as described by Riemann and Schrage, 1978) may serve as food for the nematodes. Metabolic requirements at these low temperatures are low, (similar to those described by Grootaert and Maertens, 1976, for *Mononchus aquaticus*), and it seems possible that *E. pararmatus* maintains its low-level metabolism through uptake of dissolved organic molecules. At higher temperatures (12 °C) this uptake is probably not sufficient, resulting in poor survival; the nematode needs another food source (diatoms) to keep alive and to reproduce. At this point the type of substratum also becomes important, because in liquid cultures the nematode is not able to 'catch' the

diatoms, whereas in agar cultures (whose consistence is similar to that of the silty sediment at the sampling sites), the diatoms are easily caught and consumed. In the field, however, all the respective diatom species are attached to the sediment; this may also be responsible for the different success of *E. pararmatus* when attacking diatoms in agar or in liquid medium.

Distribution in the field

Most members of the family Diplogasteridae are terrigenous inhabitants of saprobic environments (Schneider, 1938; Schiemer, 1975). *Eudiplogaster pararmatus* is considered a terrigenous species that invaded a brackish water environment and successfully colonized the polluted mud flats in the southeast of the Ems-Dollard estuary. Development of massive *E. pararmatus* populations seems to be restricted to parts of the mud flat with rather peculiar combinations of environmental parameters. The absence of predatory macrofauna (van Arkel and Mulder, unpubl.) and of food competitors (e.g. diatom-consuming oligochaetes; Bouwman, unpubl.), combined with a low salinity (average 5 ‰ S at Station 2; Admiraal and Peletier, 1980) and a surplus of diatoms, favour the development of *E. pararmatus* at the stations close to the fresh water discharge.

Results from culture experiments with different salinities indicate that *Eudiplogaster pararmatus* reproduces best at salinities below 5 ‰ S. Riemann (1966) found a similar distribution for *E. pararmatus* in the Elbe estuary. Tolerance to anaerobic conditions and high sulphide concentrations (occurring part of the year at the sampling sites) also play a role in the distribution of nematodes (examples of comparable biotopes are mentioned by Wieser and Kanwisher, 1961; Teal and Wieser, 1966; Schiemer, 1975; Surey-Gent, 1981). Data on tolerance of *E. pararmatus* to anaerobiosis and elevated sulphide concentrations are not available. *E. pararmatus* can survive under several extreme conditions (low temperature, low food densities, high salinities etc.) but it requires specific conditions for high rates of reproduction (low salinities, sufficient amount of edible food etc.). Possibly the vivipary of *E. pararmatus* is advantageous for survival under extreme conditions, because the first-stage juveniles are protected during early life stages (compare Surey-Gent, 1981; vivipary of *Anoplostoma viviparum*).

Population growth in situ and in cultures

In spring, the field population of *Eudiplogaster pararmatus* shows exponential growth (Fig. 6, Stations 1 and 2), which can be characterized by the intrinsic rate of natural increase (r). The highest value of r calculated from field data was 0.08; this is slightly higher than the highest rate calculated from fast growing populations in cultures (0.06 to 0.07).

Generation time of *Eudiplogaster pararmatus*, calculated for the natural habitat (12° to 18 °C), is therefore shorter than the generation time observed in cultures at comparable temperatures. Brief exposure to higher temperatures in the field, e.g. during emersion of the flats, may be responsible for this difference. No data are available on the influence of these brief exposures on the growth of *E. pararmatus*.

In general, long exposure to higher temperatures shortens the generation time (see Gerlach and Schrage, 1971; Tietjen and Lee, 1972) but when temperatures are very high, generation time lengthens again (Hopper et al., 1973; Tietjen and Lee, 1977). Higher temperatures probably stimulate the development of reproductive organs at an early life-cycle stage. Culture experiments with *Eudiplogaster pararmatus* at different temperatures confirm this: at 12 °C the growth of individual nematodes is obvious and sexual differentiation occurs after approximately 2.5 wk. When temperature increases (21 °C), the growth of individuals is less obvious but sexual differentiation already occurs after 1.5 wk; this means that at higher temperatures, all the energy available can be used for reproduction, growth ranking second.

The number of juveniles (N_e) per female, observed in the field (10 to 12) was slightly higher than that observed in cultures (8 to 10). This may also have contributed to the difference in generation time observed in cultures and the generation time calculated from field populations.

Generation time of some other nematodes with a comparable life style, are mentioned by Chitwood and Murphy (1964), Hopper and Meyers (1966b), von Thun (1968) and Gerlach and Schrage (1971). Most of these nematodes have generation times of 3 to 4 wk (in cultures) which is comparable to the generation time calculated for *Eudiplogaster pararmatus* in the field.

The growth of *Eudiplogaster pararmatus* in the field is characterized by rapid increases in spring; in summer growth stagnates. This stagnation may be caused by the fact that the composition of the diatom population changes: the numbers of *Navicula salinarum* (suitable food for *E. pararmatus*), decrease during summer, while the numbers of *N. pygmaea* (less suitable food) increase. The nematode may have to spend more energy in feeding in summer and therefore less energy will be available for reproduction, and population growth will cease (see also Admiraal et al., 1983). Decrease in the nematode population in autumn is probably the result of a combination of factors such as

low food densities and low temperatures. Reproduction does not stop completely during winter, but remains at a low level. In spring, when conditions improve (temperature rises, amount of suitable food increases), *E. pararmatus* is able to build up a dense population again.

Acknowledgements. We are grateful to Professor C. v. d. Hoek, Dr. F. Riemann and Dr. P. de Wolf, for their comments on the manuscript, to L. Hoekstra, E. Kremer and J. Smit, for providing experimental data, to M. de Jonge-Swieter and H. Peletier for determining carbon contents and to G. Kamstra for drawing the figures.

LITERATURE CITED

Admiraal, W. (1977). Influence of light and temperature on the growth rates of estuarine benthic diatoms in culture. Mar. Biol. 39: 1–9

Admiraal, W., Peletier, H. (1980). Distribution of diatom species on an estuarine mudflat and experimental analysis of the selective effect of stress. J. exp. mar. biol. Ecol. 46: 157–175

Admiraal, W., Bouwman, L. A., Hoekstra, L., Romeyn, K. (1983). Quantitative interactions between microphytobenthos and herbivorous meiofauna of an estuarine mudflat. Int. Revue ges. Hydrobiol. 68: 175–191

Bouwman, L. A. (1978). Investigations on nematodes in the Ems-Dollard estuary. Annls. Soc. zool. Belg. 108: 103–105

Bouwman, L. A. (1981). A survey of nematodes from the Ems estuary. Part 1: Systematics. Zool. Jb. (Syst.) 108: 335–385; Part 2: Species assemblages and associations, in press

Chia, F. S., Warwick, R. M. (1969). Assimilation of labelled glucose from seawater by marine nematodes. Nature, Lond. 224: 720–721

Chitwood, B. G., Murphy, D. G. (1964). Observations on two marine *Monhysterids,* their classification, cultivation and behaviour. Trans. Am. microsc. Soc. 83: 311–329

Dusenberry, D. B. (1974). Analysis of chemotaxis in the nematode *Caenorhabditis elegans* by countercurrent separation. J. exp. Zool. 188: 41–48

Es, F. B. van, van Arkel, M. A., Bouwman, L. A., Schröder, H. G. J. (1980). Influence of organic pollution on bacterial, macrobenthic and and meiobenthic populations in intertidal flats of the Dollard. Neth. J. Sea Res. 14 (4/3): 288–304

Fenchel, T. (1974). Intrinsic rate of natural increase: The relationship with body size. Oecologia (Berl.) 14: 317–326

Gerlach, S. A., Schrage, M. (1971). Life cycles in marine meiobenthos. Experiments at various temperatures with *Monhystera disjuncta, Theristus pertenuis* (Nematoda). Mar. Biol. 9: 274–280

Grootaert, P., Maertens, D. (1976). Cultivation and life-cycle of *Mononchus aquaticus.* Nematologica 22: 173–181

Heip, L., Smol, N., Absillis, V. (1978). Influence of temperature on the reproductive potential of *Oncholaimus oxyuris* (Nematodes: Oncholaimidae). Mar. Biol. 45: 255–260

Hellebust, J. A. (1974). Extracellular products. In: Stewart, W. D. P. (ed.) Algal physiology and biochemistry. University of California Press, Berkely, p. 838–863

Hopper, B. E., Fell, J. W., Cefalu, R. C. (1973). Effect of temperature on life-cycles of nematodes associated with the mangrove *(Rhizophora mangle)* detrital system. Mar. Biol. 23: 293–296

Hopper, B. E., Meyers, S. (1966a). Observations on the bionomics of the marine nematode *Metoncholaimus sp.* Nature, Lond. 209: 899–900

Hopper, B. E., Meyers, S. (1966b). Aspects of the life cycle of marine nematodes. Helgoländer wiss. Meeresunters. 13: 444–449

Jonge, V. N. de, Bouwman, L. A. (1977). A simple density separation technique for quantitative isolation of meiobenthos, using the colloid silica gel Ludox T. M. Mar. Biol. 42: 143–148

Lee, J. J., Tietjen, J. H., Mastropaolo, C., Rubin, H. (1977). Food quality and the heterogenous spatial distribution of meiofauna. Helgoländer wiss. Meeresunters. 30: 272–282

Lopez, G., Riemann, F., Schrage, M. (1979). Feeding biology of the brackish water oncholaimid nematode *Adoncholaimus thalassophygas.* Mar. Biol. 54: 311–318

Maertens, D. (1975). Observations on the life-cycle of *Prionchulus punctatus* (Cobb, 1917) (Nematodes) and some culture conditions. Biol. Jb. Dodonaea 43: 197–218

Riemann, F. (1966). Die interstitielle Fauna im Elbe Aestuar, Verbreitung und Systematik. Arch. Hydrobiol. (Suppl. Bd XXXL) 1–279

Riemann, F., Schrage, M. (1978). The mucus-trap hypothesis on feeding of aquatic nematodes and implications for biodegradation and sediment texture. Oecologia (Berl.) 34: 75–88

Romeyn, K. (1980). Een inventarisatie van de nematoden fauna van de Dollard en de rol van diatomeen als voedsel voor enkele nematoden soorten. BOEDE publ. en versl. 7

Schiemer, F. (1975). Nematoda. In: Curds, C. R., Hawkes, H. A. (eds.). Ecological aspects of used-water treatment. Vol. 1. The organisms and their ecology. Academic Press, London, p. 269–288

Schneider, W. (1938). *Diplogaster pararmatus* n. n. nebst Bemerkungen über einige andere Diplogaster-Arten. Zool. Anz. 121: 37–43

Schneider, W. (1939). Die Tierwelt Deutschlands und der angrenzenden Meeresteile. Teil 36.11. Fadenwürmer. Fischer Verlag, Jena

Schröder, H. G. J., van Es, F. B. (1980). Distribution of bacteria in intertidal sediments of the Ems-Dollard estuary. Neth. J. Sea Res. 14 (3/4): 268–287

Surey-Gent, S. C. (1981). Distribution of *Anoplostoma viviparum* (Nematoda) in Southampton water sediments. Mar. Biol. 62: 157–160

Teal, J. M., Wieser, W. (1966). The distribution and ecology of nematodes in a Georgia salt marsh. Limnol. Oecanogr. 11: 217–222

Thun, W. H., von (1968). Autökologische Untersuchungen an freilebenden Nematoden des Brackwassers. Thesis, University Kiel

Tietjen, J. H., Lee, J. J. (1972). Life-cycles in marine nematodes. Influence of temperature and salinity on the development of *Monhystera denticulata* Timm. Oecologia (Berl.) 10: 167–176

Tietjen, J. H., Lee, J. J. (1973). Life history and feeding habits of the marine nematode *Chromadora macrolaimoides,* Steiner. Oecologia (Berl.) 12: 303–314

Tietjen, J. H., Lee, J. J. (1977). Life histories of marine nematodes. Influence of temperature and salinity on the reproductive potential of *Chromadorina germanica,* Bütschli. Mikrofauna des Meeresboden 61: 263–270

Tietjen, J. H., Lee, J. J., Rullman, J., Greengart, A., Trompeter, J. (1970). Gnotobiotic culture and physiological ecology of the marine nematode *Rhabditis marina* (Bastian). Limnol. Oceanogr. 15: 535–543

Wieser, W (1953). Die Beziehung zwischen Mundhöhlenge-

stalt, Ernährungsweise und Vorkommen bei freilebenden marinen Nematoden. Arkiv Zool. 4: 439–484

Wieser, W., Kanwisher, J. (1959). Growth and metabolism in a marine nematode *Enoplus communis* (Bastian). Z. vergl. Physiol. 43: 29–36

Wieser, W., Kanwisher, J. (1961). Ecological and physiological studies on marine nematodes from a small salt marsh near Woods Hole, Massachusetts. Limnol. Oceanogr. 6: 262–270

This paper was submitted to the editor; it was accepted for printing on March 14, 1983